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Barnacle Attachment on Live *Nautilus*: Implications for *Nautilus* Growth Rate

by

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Abstract. Attachment of the barnacle *Chirona tenuis* (1.8 cm in height) onto the mid-venter of a juvenile *Nautilus pompilius* (10.7 cm in diameter) during its life permits observations on the secretory reaction of the nautilus to the presence of the barnacle and provides an estimate of the growth rate of *N. pompilius* in nature. The nautilus secreted a thick, multilayered, black film interleaved with aragonite deposits in an attempt to overgrow the barnacle; the aragonite had a spherulitic-prismatic microstructure. The age of the barnacle provides a *minimum* estimate of the rate of growth of the last nautilus whorl. Growth band counts on three wall plates average 680. If growth band formation is presumed to be semidiurnal, based on field and experimental data for other barnacles, the age of the barnacle is 340 days and represents a minimum estimate of the rate of growth of the last nautilus whorl. Judging from the spacing of chambers, about 16 chambers probably formed during this time yielding a minimum average of about 21 days per chamber.

EPIZOA ON THE SHELLS of live *Nautilus* are not uncommon and typically consist of serpulid polychaetes near the umbilicus or on the shell flanks and venter (SEILACHER, 1982). The absence of more extensive premortal incrustation may be explained by the mobile life style of *Nautilus* (STENZEL, 1964), its smooth shell covered with a thin, organic periostracum (BOTTJER, 1981), and possibly some antifouling behavior. Barnacle attachment is rare but has been observed on live *N. belauensis* from Palau (W. B. Saunders, personal communication) and on live *N. pompilius* from Fiji (B. A. Foster, personal communication).

While studying collections at the Museum of Comparative Zoology, Harvard University, I discovered a small shell of *N. pompilius* (M.C.Z. No. 138167), 10.7 cm in diameter, with a large barnacle attached to its dorsum (Figures 1, 2). The barnacle, 1.8 cm in height and 1.9 cm in diameter, has been tentatively identified by B. A. Foster from photographs as *Chirona tenuis* (Hoek). This species lives in the Indo-West Pacific and elsewhere to depths of 500 m, approximating the maximum depth of *N. pompilius*, and often occurs on the shells of gastropods (NEWMAN & ROSS, 1976, p. 50, and references therein). The nautilus was collected off Golo Island, Mindoro, Philippines, and, although other details of collection are not available, incrustation was evidently premortal as the nautilus was in the process of overgrowing the barnacle. However, the large size and position of the barnacle impeded further growth of the nautilus and may have affected its swimming and buoyancy capability. Aside from curiosity, this occurrence permits two further inquiries: documentation of the secretory reaction of the nautilus to the presence of the barnacle, and estimation of the growth rate of *Nautilus* in nature. The barnacle contains in its shell a record of its growth. By deciphering this record, an estimate of the age of the barnacle can be obtained which in turn permits an estimate of the growth rate of the nautilus.

Secretory Reaction to the Barnacle

On the dorsal part of its shell, *Nautilus* secretes a black layer or band presumably deposited by a portion of the mantle fold (JOUBIN, 1892). The black layer conforms to the shell surface, dampening out growth lines and shell irregularities. Epibionts such as serpulid worm tubes are neatly covered with a slight thickening of the black deposit. The black deposit is itself continuously overlain by an advancing layer of nacre as the animal grows, leaving only the leading centimeter or so of the black layer free of nacre (STENZEL, 1964). Thus, the black layer apparently serves to enshroud epibionts and, as JOUBIN (1892) suggested, to provide a more uniform surface for nacre deposition.

In the nautilus specimen studied, these functions were put to a severe test by the presence of the barnacle. The black layer extended onto the shell flanks and overgrew the lower edges of the barnacle walls. The black layer was thick and multilayered and was interspersed with deposits of aragonite which exhibited a botryoidal appearance under low magnification (Figure 3). Under scanning electron microscopy, these deposits revealed a spherulitic-prismatic microstructure composed of radiating crystals about 70 μm in length (Figure 4). This increase in secretory activity near the barnacle was not matched by any shell thickening at the apertural margin nor any reduction in the spacing of the last chamber (Figure 5).

Barnacle Age and *Nautilus* Growth Rate

Using epibionts that grew during the lifetime of their host to speculate about the growth rate of the host has been attempted for extinct ammonites by SCHINDEWOLF (1934). Although *Nautilus* is extant, information about its growth rate in nature, especially in juvenile animals, is sparse. DENTON & GILPIN-BROWN (1966), based on theoretical rates of gas-pressure build-up in newly formed chambers of *Nautilus macromphalus,* inferred a constant 14-day periodicity between septal formation, a figure later regarded as a minimum by COLLINS *et al.* (1980). *Nautilus macromphalus* maintained in aquaria have yielded estimates of 1–4 months between septal formation (MARTIN *et al.,* 1978; WARD *et al.,* 1981). The first estimates of the growth rate of *Nautilus* in nature, based on the activity ratio of two naturally occurring radionuclides incorporated into the shell during growth, yielded times of 25 and 75 days between septal deposition in two juvenile *N. pompilius* 8.4 cm in diameter (COCHRAN *et al.,* 1981).

Determination of the age of the barnacle attached to *N. pompilius* provides another means of estimating the natural growth rate of *Nautilus.* The barnacle settled almost exactly on the mid-line of the shell with its carinal plate oriented in the adapical direction of nautilus growth. Subsequent growth of the barnacle favored a bending toward the left flank of the nautilus and the parietal plates are shorter on this side. The basal disk is calcified and measures 1.9 cm in diameter. Below it on the shell surface, approximately 28 asymetrically skewed concentric bands radiate from the original attachment site.

The age of the barnacle yields a *minimum* estimate of the rate of growth of the last nautilus whorl. The reasons are outlined below.

(a) Depending on the position of the barnacle relative to the aperture at the time of settlement, no more than a full whorl of nautilus growth would have had to elapse before reaching its present position at the time of incipient overgrowth. According to SEILACHER (1960), a barnacle will settle on an inclined substrate with its carinal plate on top. Based on the orientation of *Chirona* (see above) and the living position of *Nautilus,* the barnacle probably settled on the venter at some distance behind the aperture, facing into the direction of swimming. Therefore, less than a full whorl of nautilus growth would have had to elapse before reaching its present position.

(b) Because the barnacle grew in both the adapical and adoral directions of nautilus growth, the nautilus actually encountered it about 6 mm or a few degrees of arc ($\sim 10°$) adapical of its original attachment site. Therefore, at most, a little less than a full whorl of nautilus growth would have had to elapse.

(c) Because the details of collection are lacking, it is possible that the barnacle died some time before the nautilus began to overgrow it. In this case, the age of the barnacle would definitely be less than the time of formation of the last whorl.

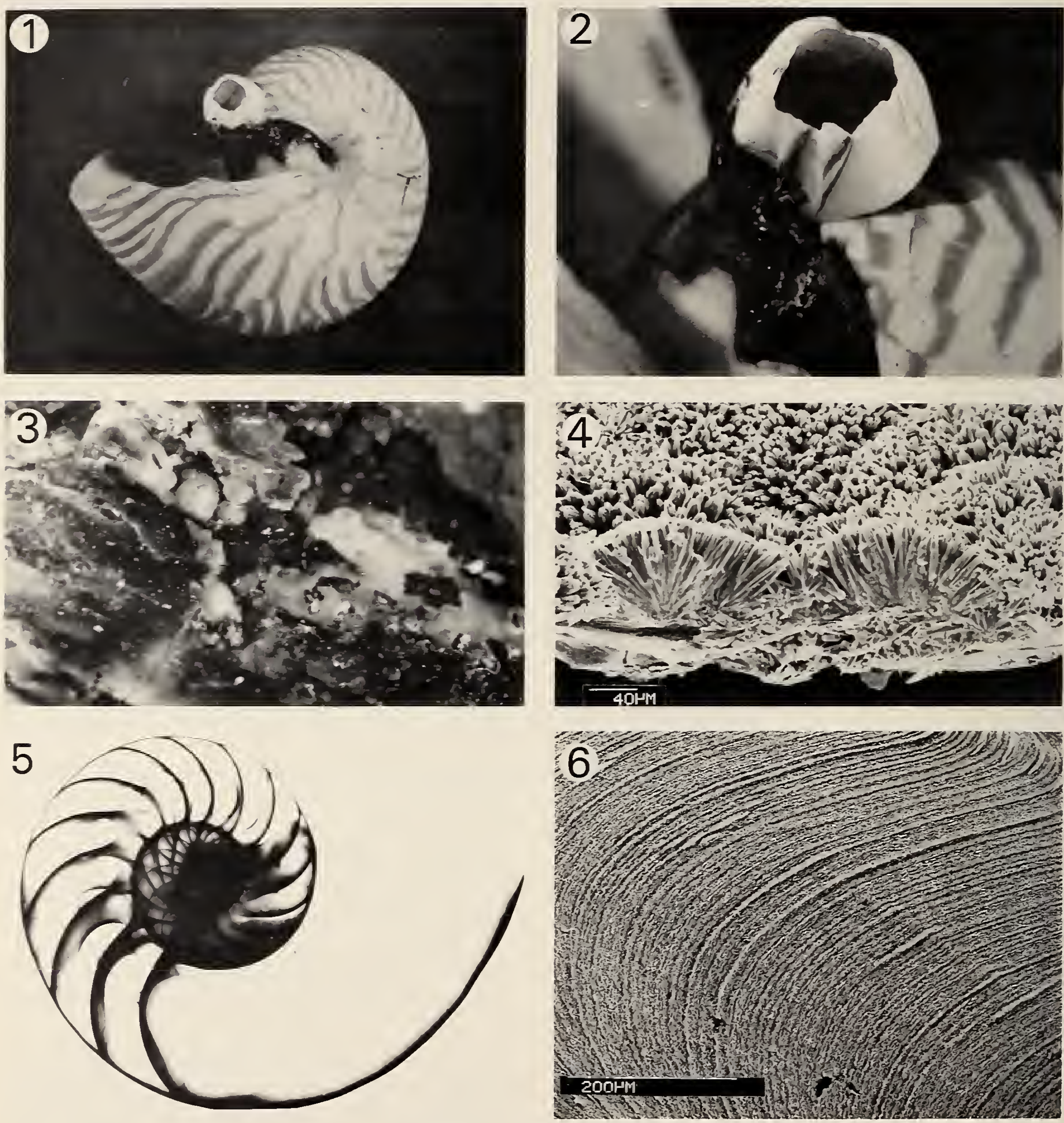
Determining the age of the barnacle presents its own problems. The most reliable growth information is contained in the form of internal growth bands visible in thin sections of the parietes (BOURGET, 1980). Observations on balanoideans reveal that growth bands are present in the outer and inner layer (sheath) of the parietes and are wide enough for counting (BOURGET, 1980). Interpretations of growth-band periodicity are based almost exclusively on field and laboratory experiments on intertidal and shallow subtidal forms, principally *Semibalanus balanoides* and *Elminius modestus.* However, regardless of environmental conditions, including total darkness and continuous immersion, the production of growth bands is semidiurnal (BOURGET & CRISP, 1975a, b; BOURGET, 1977, 1980). In fact, BOURGET (1980) speculates that semidiurnal growth band formation may be under endogenous control.

> "1.) semidiurnal bands are observed subtidally in newly metamorphosed animals; 2.) the production of semidiurnal bands is immediate after metamorphosis; 3.) the production of semidiurnal bands cannot be arrested in uniform conditions in the laboratory; 4.) bands [are] observed in subtidal species (Bourget, 1977); and finally 5.) bands are also observed in the deep-sea *Bathylasma corraliforme* sampled at a depth of 7,000 m in Ross Sea, Antarctic."

Based on these observations I will presume that the production of growth bands in *Chirona tenuis* is semidiurnal.

The growth band record in *C. tenuis* was examined on radial cross sections through three of the parietes. The wall plates were sectioned, polished, etched for about 4 minutes with EDTA, and replicated with acetate. The acetate peels were examined at 200× magnification with transmitted light. Growth bands were counted on the inner layer (sheath) of the parietes as suggested by BOURGET (1980), and varied in width from 5 to 11 μm (Figure 6). Growth bands were counted by three independent observers, and the results are tabulated in Table 1. The counts for all three parietes are similar and average 680 bands.

Presuming semidiurnal formation of growth bands, the



Explanation of Figures 1 to 6

Figure 1. The barnacle *Chirona tenuis* attached to the shell of *Nautilus pompilius* (MCZ No. 138167). Incrustation was premortal as the nautilus was in the process of overgrowing the barnacle. The nautilus measures 10.7 cm in diameter; the barnacle measures 1.8 cm in maximum height.

Figure 2. Close-up of Figure 1 showing the black layer deposited on the wall of the barnacle. The carinal plate points in the adapical direction of nautilus growth.

Figure 3. Botryoidal deposits of aragonite interlayered with the black material (magnified 17.5×).

Figure 4. Spherulitic-prismatic microstructure of aragonite deposits in Figure 3.

Figure 5. X-ray photograph of nautilus (with barnacle removed) showing regular spacing of septa.

Figure 6. Scanning electron micrograph of growth bands in *Chirona tenuis* seen on an acetate replica of a radial cross section through the inner layer (sheath) of a wall plate. Growth bands measure 5 to 11 μm.

Table 1

Counts of growth bands in three wall plates of *Chirona tenuis* (Hoek).

	Plate 1	Plate 2	Plate 3
	709	665	680
	682	669	684
	687	647	673
	683	686	684
	709	656	660
	706		696
Average	696.0	664.6	679.5
Standard deviation	13.30	14.67	12.13
Average all three plates		680.0	
Standard deviation		15.71	

age of the barnacle is 340 days. As explained, this figure represents a minimum estimate of the rate of growth of the last nautilus whorl. Chambers in this specimen are fairly regularly spaced and average 22° in angular arc (Figure 5); approximately 16 chambers would have formed during the growth of the last whorl. Therefore, the minimum average time of chamber formation for these 16 chambers is about 21 days. This figure is an average and does not imply a constant periodicity. It compares favorably with other estimates of natural growth rate based on growth of the last 6–9 chambers in two juvenile *N. pompilius* (COCHRAN *et al.*, 1981).

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LITERATURE CITED

BOTTJER, D. J. 1981. Paleoecological implications of antifouling adaptations in shelled marine molluscs. Geol. Soc. Am. Abst. with Prog. 13(7):413.

BOURGET, E. 1977. Shell structure in sessile barnacles. Nat. Can. 104:281–323.

BOURGET, E. 1980. Barnacle growth and its relationship to environmental factors. *In:* D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms. Plenum Publishers. pp. 469–491.

BOURGET, E. & D. J. CRISP. 1975a. An analysis of the growth bands and ridges of barnacle shell plates. J. Mar. Biol. Assoc. U.K. 55:439–461.

BOURGET, E. & D. J. CRISP. 1975b. Factors affecting deposition of the shell in *Balanus balanoides* (L.). J. Mar. Biol. Assoc. U.K. 55:231–249.

COCHRAN, J. K., D. M. RYE & N. H. LANDMAN. 1981. Growth rate and habitat of *Nautilus pompilius* inferred from radioactive and stable isotope studies. Paleobiology 7(4):469–480.

COLLINS, D., P. D. WARD & G. E. G. WESTERMANN. 1980. Function of cameral water in *Nautilus.* Paleobiology 6:168–172.

DENTON, E. J. & J. B. GILPIN-BROWN. 1966. On the buoyancy of the pearly *Nautilus.* J. Mar. Biol. Assoc. U.K. 46: 723–759.

JOUBIN, L. 1892. Recherches sur la coloration du tégument chez les céphalopodes, 4 me partie, Gland sécrétant le vernis noir chez le Nautile. Arch. Zool. Exper. Gén., Ser 2. 10: 319–324.

MARTIN, A. W., I. CATALA-STUCKI & P. D. WARD. 1978. The growth rate and reproductive behavior of *Nautilus macromphalus.* N. Jb. Geol. Paläont. Abh. 156:207–225.

NEWMAN, W. A. & A. ROSS. 1976. Revision of the balanomorph barnacles; including a catalog of the species. San Diego Soc. Natl. Hist. Mem. 9:1–108.

SCHINDEWOLF, O. H. 1934. Über Epöken auf Cephalopoden-Gehäusen. Paläontol. Zeitschr. 16:15–31.

SEILACHER, A. 1960. Epizoans as keys to ammonoid ecology. J. Paleontol. 34(1):189–193.

SEILACHER, A. 1982. Ammonite shells as habitats in the Posidonia Shales of Holzmaden—floats or benthic islands? N. Jb. Geol. Paläont. Mh. 159(2):98–114.

STENZEL, H. B. 1964. Living *Nautilus. In:* R. C. Moore (ed.), Treatise on invertebrate paleontology. Univ. Kansas Press and Geol. Soc. Am., Lawrence, Kansas. part K:59–93.

WARD, P., L. GREENWALD & Y. MAGNIER. 1981. The chamber formation cycle in *Nautilus macromphalus.* Paleobiology 7(4):481–493.